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GEOGRAPHIC VARIATION IN *ANOLIS BREVIROSTRIS* (SAURIA: IGUANIDAE) IN HISPANIOLA

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ABSTRACT. The nominal Hispaniolan anole species, *Anolis brevirostris* Bocourt, is considered to be comprised of four distinct parapatric sibling species: *A. brevirostris*, *A. caudalis*, *A. websteri*, and *A. marron*. These species and the subspecies of *A. brevirostris* are described.

INTRODUCTION

Anolis brevirostris Bocourt is a rather small and stocky anoline lizard that occurs within an irregular range in xeric habitats on Hispaniola and associated islets. In 1870 Bocourt named *Anolis brevirostris* from Haiti. The name fell into disuse and obscurity, with specimens of *A. brevirostris* generally being included with *A. dominicensis* Reinhardt and Lütken. Cochran (1941) described and named two satellite island subspecies of *A. dominicensis*: *wetmorei* from Isla Beata, Dominican Republic; and *caudalis* Ile de la Gonâve, Haiti. Barbour (1937) first combined *A. dominicensis* with *A. distichus* Cope. This combination was followed by Mertens (1939) who resurrected *brevirostris* as a subspecies of *A. distichus* from the vicinity of Barahona in southwestern Dominican Republic. Ernest E. Williams, at the Museum of Comparative Zoology at Harvard University, recognized that some of the forms in Haiti and the Dominican Republic associated with *A. distichus* actually pertain to another similar species, *A. brevirostris* (the differential characters were reported in Schwartz, 1968). Named forms correctly associated with *A. brevirostris* are *caudalis* Cochran and *wetmorei* Cochran. Webster and Burns (1973) used electrophoretic observa-

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tions on several proteins to assign mainland Haitian populations of "*A. brevirostris*" to three unnamed sibling species. Webster (1978a) later expanded his electrophoretic studies to include most of the remaining distribution of *A. brevirostris*. His accidental death left behind two near-final-form manuscripts on *A. brevirostris* which lack the tables, figures, and numerical data he would have prepared to give his statements full documentation. These manuscripts subsequently became available in the Third *Anolis* Newsletter (Williams, editor, 1977). Thus, as understood by Webster, the *brevirostris* complex consisted of three unnamed sibling species referred to as A, B, and C, and two named satellite island subspecies. Williams (1976) referred the mainland Haitian species B to *caudalis* Cochran and regarded species C as nominate *brevirostris*.

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Most of the specimens I have examined are in the Albert Schwartz Field Series (ASFS). A more limited amount of material has been borrowed from the American Museum of Natural History (AMNH), Museum of Comparative Zoology (MCZ), Muséum National d'Histoire Naturelle (MNHP), Florida State Museum (UF/FSM), and the National Museum of Natural History (USNM). I am grateful to the following curators and their assistants for the loan of this material: Albert Schwartz, George W. Foley, Ernest E. Williams, Jean Guibé, Walter A. Auffenberg, W. Ronald Heyer, and Ronald J. Crombie. Burt L. Monroe provided me with work space at the University of Louisville and was instrumental in facilitating loans.

METHODS

I have not considered it worthwhile to study all the available collected specimens of the *brevirostris* complex since many of the older specimens are long-preserved and now much faded and since coloration and pattern play such a major role in differentiation of the various species and subspecies. I have attempted to examine all the material which might be assignable to new taxa proposed herein and have examined all specimens designated as holotypes, syntypes, and paratypes.

The *brevirostris* complex needs fine sampling to be understood (Webster, *in litt.*, 1972); therefore I have restricted the type-locality of *A. brevirostris*. Lists of associated specimens, not from the type-locality itself, include localities and museum numbers which I have assigned to certain taxa on the basis of my examination. A list of referred specimens in Appendix 1 includes localities and museum numbers which I have assigned to taxa on the basis of provenance; specimens so listed have not been examined by myself. The probability is high that almost all lizards listed as referred specimens are correctly designated specifically and subspecifically, since they are delimited by fresh material that I have examined. Exceptional cases or uncertain allocations are noted in the text.

Various scale counts and relationships were used by Oliver (1948) to describe Bahamian populations of *A. distichus*. Schwartz (1968) applied the same counts to non-Bahamian populations. Hoping that an application of these counts to *A. brevirostris* complex members might reveal differences other than coloration and pattern between various sibling species and their subspecies, I have followed the techniques of Oliver and of Schwartz and applied them to the material I have examined. The following data were recorded on each specimen:

- 1) Snout-vent length, in millimeters.
- 2) Number of scales across the snout at the level of the second canthal scale, reckoned from the anterior border of the orbit.
- 3) Number of horizontal rows of loreal scales.
- 4) Minimum number of scales between the supraorbital semicircles.
- 5) Number of rows of scales between the interparietal scale and the supraorbital semicircles on each side [this datum written as a fraction] (e.g., 1/1 = one row of scales on each side).

6) Number of scales bordering the postfrontal laterally (see Oliver, 1948:16, for drawings showing these scales in *A. distichus*). In a small number of specimens of *A. brevirostris*, the postfrontals may extend so far laterally as to make contact with one or two of the canthals. In such instances, I have not included the canthal as a scale in contact with the postfrontal, since the condition is anomalous.

7) Number of median (usually azygous) scales posterior to the posterior-most paramedian pair of snout scales, usually restricted to the midline from the anterior border of the postfrontals posteriorly to the anterior border of supraorbital semicircle contact, thus excluding the highly variable preoccipital region. (This count differs from those of Oliver and Schwartz but is made comparable by subtracting 1 from their counts — the nearly-always present preoccipital of *A. distichus*.)

8) Number of supraorbital semicircle scales in contact with the interparietal scale. This count is partly correlated with (5), the number of rows of scales between the semicircles and the interparietals; for instance, if the latter count is 1/1, the number of supraorbital scales in contact with the interparietal will of necessity be 0/0. However, if the count of (5) is 0/0 (i.e., there are no scales between the semicircles and the interparietal) then (8) may have a fairly wide fluctuation.

9) Number of postmental scales.

10) Condition of the preoccipital region categorized as: preoccipital present (+); series of small scales bordering interparietal anteriorly which may be incomplete (ss); preoccipital present but separated from interparietal by a series of small scales (ps); multiple small scales in preoccipital region (ms); preoccipital present, but tiny (t); and preoccipital absent (—), supraorbital semicircles in contact with anterior border of interparietal.

11) Condition of nuchal patch, categorized as large, medium, reduced, or absent; dark or faint; with or without white border. A medium-sized nuchal patch is reckoned to approximate the size of the external ear opening.

The above counts and notations were taken on 770 specimens from Haiti and the Dominican Republic. Test counts taken on the number of subdigital lamellae on phalanges II and III of the fourth toe of the hind foot and the number of scales in tail verticils were discontinued as no significant variation was observed. Complete

scale counts for each specific and subspecific samples are given in Table 1, where frequencies and modes are also shown. The reader is referred to this table for details of scutellar variation.

A few scale counts as modes, not as absolute counts, have proven to be useful in defining the species and subspecies. The degree of overlap between various counts for different samples is generally extensive, so that it is impossible to identify the species and subspecies of a particular specimen solely on the basis of any set of counts. Therefore reliance must be placed on such features as dewlap pattern and coloration, nuchal patch pattern, and coloration and pattern of the head and body in general. These additional data were taken from series having field notes on coloration. (As mentioned above, museum specimens as such have very limited utility.) The colors of many dewlaps were noted in the field with reference to Maerz and Paul (1950).

THE *ANOLIS BREVIROSTRIS* COMPLEX

As noted in the Introduction, the *brevirostris* complex is presently understood to consist of three sibling species. The material on which the name *A. brevirostris* was based had its provenance merely as "Haiti". I have examined the three syntypes loaned by the Muséum National d'Histoire Naturelle in Paris and find that two are *A. distichus*. The remaining one is *A. brevirostris* and has similarities to those lizards which are currently called "Species C". With the recognition of new species within the *brevirostris* complex, it is appropriate to restrict the type-locality of *A. brevirostris* in order to clarify my concept of the species; I hereby designate the vicinity of Fond Parisien, Département de l'Ouest, Haiti, as the type-locality of *A. brevirostris*. It is not unlikely that the original specimens, collected by M. Braconnier, actually came from the vicinity of Port-au-Prince, for the Haitian capital has long been a prominent Caribbean seaport. No *brevirostris* complex anoles have been collected recently from Port-au-Prince, yet sibling species A, B, and C have all been collected within 20 km airline of that city. Therefore I have chosen to designate the type-locality of *A. brevirostris* in the known distribution of Species C. Henceforth in this paper, *A. brevirostris* will refer only to Species C and "*A. brevirostris*" will refer to the complex in general.

Table 1. Meristic data for eight scale counts of six populations of anoles of the *Anolis brevirostris* complex. N=number of specimens examined. The first vertical column indicates the variation in each character, with the frequencies indicated thereafter in the following vertical columns. Modes are set in *italics*, and the percentage of the sample having the modal condition (or bi- or tri-modes) is indicated in parentheses. Means ($\bar{x}$) are indicated only for number of postmental scales.

	<i>A. b. brevirostris</i>	<i>A. b. deserticola</i>	<i>A. b. wetmorei</i>	<i>A. caudalis</i>	<i>A. marron</i>	<i>A. websteri</i>
N	146	179	232	131	31	51
Scales across snout						
3	—	—	—	1	—	—
4	79 (54%)	137 (77%)	100 (43%)	34	19 (61%)	33 (65%)
5	35	24	61	42	6	8
6	26	16	50	48 (37%)	6	10
7	4	1	5	3	—	—
8	1	—	5	3	—	—
Loreal rows						
3	5	—	1	1	—	—
4	89 (61%)	73	92	82 (63%)	13	27 (53%)
5	51	100 (56%)	127 (55%)	44	16 (52%)	24
6	—	5	12	3	2	—
7	—	—	—	1	—	—
Scales between semicircles and interparietal						
0/0	26	88 (49%)	51	43	13 (42%)	7
0/1	17	19	26	18	4	2
1/1	71 (49%)	65	121 (52%)	54 (41%)	11	32 (63%)
1/2	15	2	15	9	2	7
2/2	14	4	18	6	1	3
2/3	—	—	—	1	—	—
0/2	1	—	—	—	—	—

Table 1 (continued)

Scales in contact with interparietal	0/0	100 (69%)	72 (40%)	156 (57%)	70 (53%)	14 (45%)	42 (82%)
	0/1	18	17	25	18	4	2
	1/1	17	37	29	32	5	7
	1/2	5	24	10	7	6	—
	2/2	2	21	11	4	1	—
	2/3	1	5	1	—	1	—
Lateral postfrontal contact	1/2	2	—	—	—	—	—
	2/2	10	133 (75%)	80 (35%)	88 (68%)	18 (56%)	21 (41%)
	2/3	31	21	45	24	6	9
	3/3	79 (54%)	17	80 (35%)	12	5	14
	3/4	16	2	15	5	1	5
	4/4	5	2	2	—	1	—
	2/4	2	1	7	2	—	1
	2/5	—	1	—	—	—	—
	4/5	—	—	1	—	—	1
Median head scales	0	32	33	53	17	7	5
	1	63 (43%)	69 (39%)	100 (43%)	35	10 (32%)	18 (35%)
	2	31	69 (39%)	58	44 (34%)	10 (32%)	14
	3	16	5	16	27	2	11
	4	3	2	5	7	2	1
	5	—	—	—	1	—	2

Table 1 (continued)

	<i>A. b. breviostris</i>	<i>A. b. deserticola</i>	<i>A. b. weimerei</i>	<i>A. caudalis</i>	<i>A. marron</i>	<i>A. websteri</i>
Postmentals						
2	2	2	—	2	—	1
3	2	—	5	4	1	4
4	68 (47%)	30	60	52 (40%)	5	12 (24%)
5	44	46 (26%)	82 (35%)	44	9 (29%)	12 (24%)
6	24	46 (26%)	52	23	9 (29%)	12 (24%)
7	6	33	24	4	5	7
8	—	16	6	1	2	2
9	—	5	1	—	—	1
x	4.7	5.8	5.2	4.7	5.6	5.3
Condition of preoccipital region						
t	6	49	15	4	2	2
s	—	11	6	4	2	2
ms	75 (52%)	75 (42%)	128 (55%)	35	17 (55%)	34 (67%)
ps	23	6	15	13	1	6
+	6	7	12	13	2	5
	34	31	56	67 (46%)	7	2

"ANOLIS BREVIROSTRIS" NATURAL HISTORY

Anoles of the *brevirostris* complex and *A. distichus* are usually allotopic, but broadly sympatric. However, in certain localities where the generally xeric habitat of "*A. brevirostris*" intergrades with the generally mesic habitat of *A. distichus*, the two are precisely syntopic. In these situations hybridization is known to occur, to varying degrees, producing in the analyzed cases sterile offspring (Webster, 1978b).

"*A. brevirostris*" is cryptic. A generalized, composite head and dorsal pattern for the entire complex consists of: barred limbs and tail, two longitudinal dorsolateral stripes, an interocular bar, interparietal U, interocular V, and a series of five to seven dorsomedian chevrons pointed posteriorly. The first chevron is an internuchal patch. The upper longitudinal stripe extends from the angle of the jaw posteriorly to the level of the scapulae. Localized emphasis of this stripe forms the nuchal patch and scapular stripe. The lower longitudinal stripe extends from beneath the jaw across the shoulder to the hindlimbs. The pigmentation for the median dorsal stripe with chevrons is darker than the region below the upper dorsolateral stripe. All the markings are in general, faint with poor contrast, and interrupted outlines.

The largest specimens of "*A. brevirostris*" are from inland northern Haiti. In the Vallée de l'Artibonite in the vicinity of Dessalines and Pont Sondé, males reach a snout-vent length of 51 mm and females 47 mm. In general, females of all populations reach a maximum size about 4 to 8 mm less than do males. The smallest specimens are from Isla Beata off the coast of the Península de Barahona, where males reach a snout-vent length of only 43 mm and females 38 mm.

"*A. brevirostris*" has an extensive but narrow distribution on Hispaniola. It occupies situations varying from mesic moderate elevations (Sierra Martín García, 915 m) to extreme xeric regions (Cul de Sac-Valle de Neiba plain, at or below sea level). Typically an inhabitant of xeric habitats, "*A. brevirostris*" prefers the larger trees of xeric woods and flourishes in the proximity of springs and in the conspicuously taller *Acacia* around villages. It is present through much of the low (often dense) *Acacia* scrub between the more favorable habitats.

In the mesic regions along the east coast of the Península de Barahona, "*A. brevirostris*" is frequently observed on fenceposts in variegated sun and shade situations as well as on trees. In addition, "*A. brevirostris*" has been collected on vines, shrubs, trees, and on a cliff face 90 m above the ocean. In the extreme xeric region of the Cul de Sac-Valle de Neiba plain it is more frequently associated with *Cocos*, being found diurnally on the ground under palm logs, stacks of palm fronds, in coconut piles, and in *Cocos* trash. It is possible that in this region "*A. brevirostris*" resorts to such situations for nocturnal retreats. Generally, when it is found asleep it is one to three m above the ground on vines, shrubs, or particularly *Acacia*.

SYSTEMATIC ACCOUNT

Anolis brevirostris brevirostris Bocourt

Anolis brevirostris Bocourt, 1870, Nouv. Arch. Mus. Hist., Paris 6:11.

Lectotype. MNHP 2467B, an immature female collected by M. Braconnier.

Type-locality. "Haiti"; restricted here to within 5 km of Fond Parisien, Dépt. de l'Ouest, Haiti.

Associated specimens. *Haiti*, Dépt. de l'Ouest, Léogâne (MCZ 13781); Fond Michelle, 549 m (ASFS V37159); 7.4 km W. Thoma-zeau (ASFS V8156); Terre Rouge (ASFS V24266-94); La Source, Fond Parisien on edge of Etang Saumâtre (ASFS V8129-31); Source Fond Parisien, 1.6 km NE Fond Parisien (ASFS V36921-58); 3.2 km NW Fond Parisien (ASFS V36980-81); *Dominican Republic*, *Independencia Province*, Tierra Nueva (ASFS V42367-88); 10.4 km NE Jimaní (ASFS X9506); 5 km N Jimaní (ASFS V35476-77); Boca de Cachón (ASFS V4379, ASFS V39719-41); Las Baitoas (ASFS V14310-22); 6 km NW Duvergé (ASFS V17142-46); 5 km NNW Duvergé (ASFS X9937); just E Duvergé (ASFS V23274); Los Saladillos (ASFS V41744-45).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 48 mm, females to 45 mm snout-vent length); dorsum dark gray to medium gray and brown; dewlap pale, monochromatic, shades of orange, peach, yellow, gray, olive, and brown; nuchal patch variable, from reduced but dark, with no white border to medium and dark, with a white border; modally 1/1 scales between the supraorbital semicircles and the

interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally a single row of small scales bordering interparietal anteriorly; modally 3/3 scales in contact laterally with the postfrontals (Species C of Webster and Burns, 1973).

Distribution. Hispaniola: in the Dominican Republic from Independencia Province (Las Salinas), the Valle de Neiba, west into the Haitian Cul de Sac Plain, Dépt. de l'Ouest (Daspinasse) and an isolated population on the Cap de Léogâne, Dept. de l'Ouest (Léogâne).

Description of lectotype. The lectotype has the following measurements and scale counts: snout-vent length 34 mm, tail 55 mm, four scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and the interparietal, 0/0 supraorbitals in contact with the interparietal, a single row of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, six postmentals. Syntypes MHNP 2467 and 2467A are both *A. distichus*.

Variation. Scale counts for the series of 146 specimens of *A. b. brevirostris* are shown in Table 1.

The dorsum and markings of *A. b. brevirostris* vary clinally. In the east (Duvergé), the dorsum is medium gray-brown. The interocular bar is present. The interparietal U and interocular V are often present. Dorsomedian chevrons are occasionally found. Both dorsolateral stripes are present in reduced form. The upper remains as a scapular stripe and a nuchal patch is medium and dark, with a white border. The lower dorsolateral stripe is irregularly interrupted. The limbs and tail are barred. The more western the population, the more vague are the head and body markings, and the darker and more uniform gray the dorsum. At the western extreme the interparietal U and the dorsomedian chevrons are absent. The tail and limbs are vaguely barred. The upper dorsolateral stripe is reduced, often to a scapular spot and a reduced, dark, borderless nuchal patch.

Three geographical regions of dewlap variation in *A. b. brevirostris* are discernible. At the western extreme (Daspinasse to Thoma-zeau) dewlaps are pale, monochromatic in hues of gray, brown, yellow, yellow-gray, cream, peach, and rarely white. In the southern Cul de Sac Plain and Valle de Neiba the dewlaps are predominately pale orange and peach. Dark and bright orange dewlaps have been noted in the vicinity of Fond Parisien and Duvergé. Bicolored dewlaps, pale orange with a thin pale yellow margin, are found within

this region from Las Salinas to 10 km west of Duvergé. A third region, the northern Valle de Neiba between Etang Saumâtre and Lac Enriquillo, has predominately pale yellow and yellow-brown dewlaps. Hues noted for *A. b. brevirostris* are: Pl. 916, Pl. 9K5, Pl. 14Cl, and Pl. 14H5.

The isolated population on the Cap de Léogâne is represented by a single specimen (MCZ 13781) collected by G. M. Allen, August 1919. The dorsum is a medium to dark brown with a dark colored and medium sized nuchal patch with a white border. The limbs and tail are barred. The scapular stripe is present, but other markings are obscured by the dark dorsum. Scale counts for the Léogâne *A. b. brevirostris* are: six scales across the snout, four loreal rows, supraorbital semicircles in contact, 1/1 scales between semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 4/3 scales in lateral contact with postfrontals, four median head scales, four postmentals, and preoccipital present but separated from interparietal by a row of small scales.

Anolis brevirostris deserticola, new subspecies

Holotype. MCZ 132391, an adult male.

Type-locality. 2.1 km S San José de Ocoa, Peravia Province, Dominican Republic one of a series taken 19 November 1971, collected by natives. Original number ASFS V34034.

Paratypes (all from *Peravia Province, Dominican Republic*). ASFS V34031-33, ASFS V34035-67, same data as holotype; ASFS V724-25, 1.8 km S San José de Ocoa, 24 August 1963, A. Schwartz; ASFS V15615-25, San José de Ocoa, 3 August, 1968, native collectors.

Associated specimens. *Dominican Republic, La Estrelleta Prov.*, 2.5 km NW El Llano, 365 m (ASFS V31510-12); *San Juan Prov.*, 6.8 km NW Juan Herrera, 490 m (ASFS V31401); 1.7 km NW Sabaneta, 670 m (ASFS V31394); 10.2 km S Las Matas de Farfán, 550 m (ASFS V31327, ASFS V31468); 7.8 km NW Vallejuelo, 732 m (ASFS V31312); 1 km W Sabana Alta (MCZ 125547-48); SE Sabana Alta (MCZ 125554-55); 3 km W Guanito (MCZ 128236-47); 15 km SE San Juan (ASFS V412, ASFS V470-86); *Azua Prov.*, Padre las Casas (MCZ 58474-76); Sierra Martín García, Mt. Busú, 610-854 m (ASFS V31214-24); Sierra Martín García, above Barreras, ca. 915 m (ASFS V21174-202); Barreras, 10 km SW Puerto Viejo (ASFS V21110-16); *Peravia Prov.*, 3-5 km S San José de

Ocoa (ASFS V21396-97); 14.2 km S San José de Ocoa, 396 m (ASFS V715); 16.2 km S San José de Ocoa, 396 m (ASFS V712); 10 km S Los Ranchitos (ASFS V15627); 19 km NW Bani (ASFS V15632); Limonal (ASFS V14921-28); *Barahona Prov.*, west side Punta Martín García (ASFS V111-16); 3.2 km NE Fondo Negro (ASFS X9688); 4 km SE Canoa (ASFS V40785); 15 km ESE Canoa (ASFS V40796); 0.8 km NE Cachón, 122 m (ASFS V30749); 7.5 km E Cabral (ASFS X9604-05); *ca.* 3 km E Cabral (ASFS V20540-41); 11.8 km S Cabral, 701 m (ASFS X9849-53); 12.3 km S Cabral, 640 m (ASFS X9834-37).

Definition. A subspecies of *A. brevirostris* characterized by: moderate size (males to 48 mm, females to 45 mm snout-vent length); dorsum medium gray-brown to medium brown; venter white; dewlap bicolor, red-orange basal spot, margin cream or pale yellow to pale, or monochromatic, peach, salmon, or yellow; nuchal patch large and dark, with white border; modally 0/0 scales between the supraorbital semicircles and interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally one or more rows of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with the postfrontals.

Distribution. Dominican Republic Valle de San Juan (El Llano, La Estrelleta Prov.), east onto the southern slopes of the Sierra de Ocoa and to the Llanos de Azua (Limonal, Peravia Prov.) and south onto the northern slopes of the Sierra de Baoruco (south of Cabral, Barahona Prov.).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 45mm, tail (broken) 48mm, four scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, preoccipital absent, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, seven postmentals.

Variation. Scale counts for the series of 179 *A. b. deserticola* are shown in Table 1.

The dorsum of *A. b. deserticola* is medium gray-brown to medium brown. The head markings are distinct and generally include the interocular bar, parietal U, and interocular V. Dorsomedian chevrons are absent, except for the internuchal chevron which is rare. The lower dorsolateral stripe is absent. The upper is present and extends from the scapula to the hindlimbs in an interrupted

pattern. The nuchal patch is large and dark, with a white border. The limbs and tail are barred. The venter is white to pale yellow with pale yellow on the underside of the tail. The dewlap is uniformly pale yellow, peach, or salmon to bicolor peach or red-orange with a pale yellow or cream margin; hues noted for the dewlap are: P1. 10D8, P1. 18F1, P1. 17E1, with centers of P1. 5B12 and P1. 6B11.

The dorsum is a darker gray and the markings most distinct in specimens from the Sierra Martín García and from the southern slopes of the Sierra de Ocoa. The browner dorsum and least distinct markings characterize specimens from the eastern Valle de San Juan (San Juan).

Seven specimens collected west of San Juan are noteworthy. The samples are small (one to three each) and were collected in ravines peripheral to the Valle de San Juan. The preoccipital is present in 71% of the specimens—significantly different from all other *A. b. deserticola*. The nuchal patch is reduced to absent.

Scale counts for specimens from the moderate elevations between Lago de Rincón and the Bahía de Neiba and along the northern slopes of the Sierra de Baoruco are intermediate between those of *A. b. deserticola* to the north and *A. b. wetmorei* to the south. The scale counts and dewlap more closely favor *A. b. deserticola* and have thus been included with them.

Anolis brevirostris wetmorei Cochran

Anolis dominicensis wetmorei Cochran, 1931, Proc. Biol. Soc. Washington 44:89.

Anolis brevirostris wetmorei: Schwartz, 1968, Bull. Mus. Comp. Zool. 137(2): 257.

Holotype. USNM 83881, an adult male, 13 May 1931, collected by A. Wetmore and F. C. Lincoln.

Type-locality. Isla Beata, Dominican Republic.

Associated specimens. Dominican Republic, Barahona Prov., Barahona (ASFS X9530-60, ASFS V14017-38, ASFS X9456-58); 5 km S Barahona (ASFS V20545-48); 6 km SE Barahona (ASFS V40787-88); 6.6 km SW Barahona, 137 m (ASFS V30240-43, V30418-19); 15 km SW Barahona (ASFS V40781-83); 5.3 km NE La Ciénaga (ASFS X9379-81); 6.4 km SW La Ciénaga, 46 m (ASFS V39858); 9 km SW La Ciénaga, 91 m (ASFS V42710); 2 km NW Paraíso (ASFS V17-24); 1 km NE Paraíso, Río Nizaito (ASFS

V40762-71); 1 km W Paraíso (ASFS V40772-80); 7.7 km W Paraíso, 152 m (ASFS V30928-31); 17.9 km NE Caletón (ASFS V30790-802); Los Patos (ASFS V16926); 6 km N Enriquillo, 427 m (ASFS V42190-209); 2.2 km NE Enriquillo (ASFS V14078-80); *Pedernales Prov.*, 21 km SW Enriquillo (ASFS X9416); 8 km NE Oviedo (viejo) (ASFS X9964-65); 7 km N Oviedo (viejo) (ASFS V23121); 5 km NE Oviedo (viejo) (ASFS V14073-75); 3 km NW Oviedo (nuevo) (ASFS V40678-87, ASFS V40471-82); 7 km N, thence 20 km SE Cabo Rojo, 183 m (ASFS V29769-70); 7 km N, thence 17.6 km SE Cabo Rojo, 152 m (ASFS V30088-89); 2 km E turn to Cabo Rojo (MCZ 128257); behind Cabo Rojo police station (MCZ 143407-08); 21 km NE Cabo Rojo, 396 m (ASFS V16782-85); 21.2 km N Cabo Rojo on Alcoa mine road, 440 m (MCZ 143403-04); L'Eglise, near La Mercedes (ASFS V21510); 10 km N Pedernales, 244 m (ASFS V30115-17); 4 km SE Pedernales (ASFS V16729-30); south center of Pedernales (ASFS V29846); Pedernales (ASFS V2505-06, ASFS V2919); *Isla Beata* (ASFS V2670-71, UF/FSM 36969-70, MCZ 37520, MCZ 58695-702, AMNH 41414, AMNH 41416-18, AMNH 44854-58); just E Punta Beata (ASFS V17220); *Haiti, Dépt. de l'Ouest*, near Saltrou (MCZ 49274-79); 4 km NNE Marigot, 61 m (ASFS V37372-77).

Definition. A subspecies of *A. brevirostris* characterized by: large size (males to 50 mm, females to 45 mm snout-vent length); dorsum pale grayish tan to gray to tan to brown to mottled greenish tan; venter white to yellow; dewlap color very variable from locality to locality (see below); nuchal patch reduced and gray to brown with no white border to large and dark with white border; modally 1/1 scales between supraorbital semicircles and interparietal; modally 0/0 supraorbitals in contact with interparietal; modally a single row of small scales bordering the interparietal anteriorly; bimodally 2/2 or 3/3 scales in contact laterally with postfrontals.

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 43 mm, tail (broken) 62 mm, five scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, a single row of small scales bordering interparietal anteriorly, 3/3 scales in lateral contact with postfrontals, three median head scales, five postmentals.

Variation. Scale counts for the series of 232 *A. b. wetmorei* are shown in Table 1.

Distribution. Hispaniola: in Haiti from the Dépt. de l'Ouest (Marigot), the southern coast of the Tiburon Peninsula east across the southern portion of the Dominican Península de Barahona (Enriquillo), Isla Beata, and north along the eastern coast of the Península de Barahona to the city of Barahona.

A. b. wetmorei varies geographically. On Isla Beata, whence *wetmorei* was first described, the dorsum is nearly uniform tan or light gray. In general the head and body markings are faint to absent. The interocular bar is faint and the interocular V is reduced to a short postocular stripe. The dorsomedian chevrons and dorsolateral stripes are absent. The nuchal patch is present and varies from large and dark to reduced and gray, but always with a white border. The limbs and tail are faintly barred. The venter is whitish and the dewlap is pale yellow.

On mainland Hispaniola *wetmorei* dewlaps vary from pale yellow to bicolored yellow with an orange central spot to deep orange or red-orange. However, regionally the variation is less extreme, favoring either the deep orange, red-orange, and bicolored orange with a thin pale margin (Enriquillo to la Ciénaga and Pedernales to Cañada la Cerca) or the pale yellow to yellow with orange blush basally characteristic of the remainder of the extensive *wetmorei* distribution. The full range of variation has been observed at the northeastern distribution extreme, Barahona, and at the regional interfaces at Pedernales, La Ciénaga, and south of Enriquillo.

The eastern orange-dewlap *wetmorei* have a dorsum that is pale greenish tan to tan. The markings of the head and body are cryptic to the point that the dorsum has a woodgrain pattern. The interocular bar is regularly present. The interparietal U is wide and dark. Mediandorsal chevrons are occasionally present, although most often they are reduced to dorsomedian spots or are absent. The upper and lower dorsolateral stripes are interrupted to absent. The legs and tail are lightly barred. The nuchal patch is reduced and faint, often gray, tan, or reddish brown, and with no white border. Hues noted for the dewlap in this series are: P1. 10I7, P1. 10G11, P1. 3F12, P1. 4B11, and P1. 11J8.

The western orange-dewlap *wetmorei* are similar to the eastern, but there are no reports of any green in the dorsal color. The markings have greater contrast. The scapular stripe is long and there are remnants of the lower dorsolateral stripe. P1. 10C10 is the only hue noted for the dewlap.

The yellow-dewlap *wetmorei* are in general more conspicuously marked, except in the vicinity of Oviedo where the dorsum is a darker and grayer version of *wetmorei* on Isla Beata. The nuchal patch for these populations is highly variable, from large and dark with a white border to reduced and faint with no white border. Additional hues noted for the dewlaps are: P1. 10F1, P1. 11F3, P1. 11E1, with P1. 11B10 and P1. 11O7 centrally.

Anolis caudalis Cochran

Anolis dominicensis caudalis Cochran, 1932, Proc. Biol. Soc. Washington 45:185.

Anolis brevirostris caudalis: Schwartz, 1968, Bull. Mus. Comp. Zool. 137(2):257.

Holotype. USNM 76801, an immature male, March 1929, collected by A. J. Poole and W. M. Perrygo.

Type-locality. Nan Café, Ile de la Gonâve, Haiti.

Paratypes. Haiti, Ile de la Gonave, USNM 76799-800, same data as holotype; USNM 77080-82, Pointe à Raquettes, "1927", W. J. Eyerdam; USNM 80388-89, 8.3-16.7 km inland Anse-à-Galets, 23 March 1930, L. H. Parish and W. M. Perrygo; Ile de la Petite Gonâve, USNM 80390, 23 March 1930, L. H. Parish and W. M. Perrygo.

Associated specimens. Haiti, Dépt. de l'Ouest, Trou Forban (ASFS X1939, ASFS V8204-14); 3.5 km E Trou Forban (ASFS X4001-03); 0.3 km NE Carries, Ouanga Bay Hotel (ASFS V36876-82); 4 km N Arcahaie (MCZ 125008-18); 3 km SE Arcahaie (ASFS V43778-81); 6 km N Duvalierville (MCZ 125022-37); 1.4 km SE Duvalierville (ASFS V36872-74); 6 km SE Duvalierville (ASFS V9834-36); Ile à Cabrit, 6 km airline SE Duvalierville (ASFS V9853-56, ASFS V44806-25); Source Matelas (MCZ 125019-21); Dépt. du Sud, Presqu'île de Baraderes, vicinity of Grand Boucan (ASFS V26342-48); 4.2km W Jérémie (USNM 59255-56); Ile de la Gonâve, Source Picmi, above Picmi (ASFS V26610-15, ASFS V26652); Anse-à-Galets (ASFS V22413-22); Etroits (ASFS X2410-15).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 48 mm, females to 44 mm snout-vent length); dorsum medium brown to light gray-tan to light gray; venter pale yellow; dewlap highly variable from uniformly

white, yellow or yellow-gray to bicolor yellow with red or orange centers to bicolor gray-green with rusty centers; nuchal patch medium, dark with white border; modally 1/1 scales between the supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally preoccipital present; modally 2/2 scales in contact laterally with the postfrontals (Species B of Webster and Burns, 1973).

Distribution. Haiti: Dépt. de l'Ouest, from Trou Forban south along the coast of the Canal de St. Marc to the Baie de Port-au-Prince (Source Matelas); Ile de la Gonâve; Ile de la Petite Gonâve; and two isolated populations on the northern shore of the Tiburon Peninsula (Dépt. du Sud: Presqu'île de Baraderes and Jérémie).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 42 mm, tail broken, six scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, preoccipital region with five small scales with an incomplete row of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, five postmentals.

Variation. Scale counts for the series of 131 *A. caudalis* are shown in Table 1.

The dorsum of *A. caudalis* is medium brown to light gray; the lightest specimens examined are from Anse-à-Galets, Ile de la Gonâve. The head markings are generally absent. Dorsomedian chevrons are absent. The nuchal patch is large and dark with a white border. The scapular stripe is short but distinct. The remainder of the dorsolateral stripes are reduced, interrupted, and vague to absent. The limbs and tail are weakly barred. The venter is pale yellow. The dewlap color is highly variable from uniformly white, yellow, yellow-gray, or gray-green, to bicolored white or yellow with variable orange centrally to bicolored yellow-green or gray-green with yellow, mustard, rusty, or darker gray-green centers. Hues noted for the dewlap color are: Pl. 12E1, Pl. 10C1, and Pl. 6K10 centrally with Pl. 10I1 and Pl. 17G1 peripherally.

At the northern mainland extreme of *A. caudalis* (Trou Forban) the dewlap is uniformly white or pale yellow to bicolored with a small orange basal spot. There is a clinal increase in the size and intensity of the orange spot the farther south along the coast (Webster and Burns, 1973). However, the extent of the orange, even at the

southern mainland extreme (Source Matelas), is not so great as that of *A. websteri*. Two exceptions to this general cline are recorded. At Trou Forban, one series (ASFS V8204-14) had dewlaps gray to greenish gray with mustard or darker gray-green centers. On the Ile à Cabrit in the Baie de Port-au-Prince the dewlaps are gray-green.

On Ile de la Gonâve no such cline exists, and the dewlap color is variable and includes all dewlap colors described above for *A. caudalis*.

The two disjunct populations of *A. caudalis* are of particular interest. Jérémie *caudalis* is represented by only two specimens (USNM 59255-56) collected by Henderson and Bartsch, 10 April 1917. The dorsum is a faded gray-tan, with a dorsomedian stripe and short scapular stripe. The nuchal patch is large and dark with a white border. The limbs and tail are barred. The head has a faint interocular bar, short ocular stripe, and a broad and dark interparietal U. Scale counts for these two *caudalis* are: six scales across snout, four loreal rows, supraorbital semicircles in contact, 0/0 and 1/1 scales between semicircles and interparietal, 0/0 and 1/1 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, no median head scales, and preoccipital present.

The other disjunct population, Grand Boucan *caudalis*, is represented by seven specimens (ASFS V26342-48) collected by Richard Thomas and natives, 4 August 1971. Of the three known disjunct populations of "*A. brevirostris*" on the Tiburon Peninsula, only Grand Boucan *caudalis* have dewlap color notes. The dewlaps are colored "pale (greenish) with faint basal dull yellow smudge". The dorsum is medium to dark brown with a scapular stripe. The lower dorsolateral stripe is discernible. The interparietal U and interocular bar and V are present. The limbs and tail are barred. The nuchal patch is large and dark with a white border. Grand Boucan *caudalis* differ from mainland and Gonâve *caudalis* in two modal scale counts: five scales across the snout and three median head scales. The preoccipital, although present, is fragmented into multiple scales in three of seven specimens.

Anolis marron, new species

Holotype. MCZ 124732, an adult male.

Type-locality. Jacmel, Département de l'Ouest, one of a series taken 15 June 1970, collected by T. P. Webster.

Paratypes. MCZ 124730-31, MCZ 124733-36, same data as holotype.

Associated specimens. Haiti, Dépt. de l'Ouest, Marigot (MCZ 124723-29); 3.2 km W Marigot (ASFS V9771-78); 4.8 km E Cayes Jacmel (ASFS V9711-16); 8 km W Jacmel (ASFS V9696-97); Terre Noire, 19.2 km SW Jacmel (ASFS V37509).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 50 mm, females to 42 mm snout-vent length); dorsum pale gray and tan to medium brown; venter pale yellow to off-white; dewlap uniformly olive-gray to bicolor tan with reddish center; nuchal patch large and dark with faint white border; modally 0/0 scales between supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally one or more rows of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with postfrontals.

Distribution. Haiti; the southern coast of the Tiburon Peninsula, from Marigot west to Terre Noire.

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 47 mm, tail 62 mm, four scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and the interparietal, 2/1 supraorbitals in contact with the interparietal, a series of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, five postmentals.

Variation. Scale counts for the series of 31 *A. marron* are shown in table 1.

The dorsum of *A. marron* is pale gray and brown to medium brown. A thin interocular bar is regularly present, but other head markings are vague or absent. The dorsomedian chevrons are reduced to small dorsal spots or are absent in all but the darkest specimens. The thin, dark scapular stripe broadens and becomes less distinct posteriorly. The lower dorsolateral stripe is interrupted and vague. The nuchal patch is large and dark with a white border. The limbs and tail are barred. The venter is pale yellow to off-white. The dewlap is either uniformly dark olive-gray or bicolored tan with a reddish center; hues noted for the dewlap are: P1. 15H5, P1. 6B10, and P1. 6C10.

Anolis websteri, new species

Holotype. MCZ 132390, an adult male.

Type-locality. 7.4 km NW Dessalines, Département de l'Artibonite, Haiti, one of a series taken 8 July 1974, collected by natives. Original number ASFS V39323.

Paratypes. ASFS V39322, ASFS V39324-37, same data as holotype.

Associated specimens. Haiti, Dépt. de Nord Ouest. Môle St. Nicholas (MCZ 63143-53); Dépt. de l'Artibonite, 6.7 km NW Gonaïves (ASFS V39295-302); 1 km NE Pont Sondé (ASFS V39342-50); Bains de Amani-y (ASFS V36900-03, ASFS V43742); 2.6 km NW Montrouis (ASFS V36888-89).

Definition. A sibling species of the *A. brevirostris* complex characterized by: large size (males to 51 mm, females to 47 mm snout-vent length); dorsum medium to dark gray and brown; venter bright yellow to yellow-orange; dewlap orange with a thin pale yellow edge; nuchal patch large and dark with no white border; modally 1/1 scales between the supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with interparietal; modally a single row of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with postfrontals. (Species A of Webster and Burns, 1973).

Distribution. Haiti; from the Dépt. de Nord Ouest (Môle St. Nicholas) and northwestern Dépt. de l'Artibonite (Marché aux Poteux; between Gonaïves and Ennery), south into the Vallée de l'Artibonite (Dessaliens and Pont Sondé) and along the coast of the Golfe de la Gonâve to Pointe de Montrouis (Montrouis).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 47 mm, tail 70 mm, five scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, a single row of small scales bordering interparietal anteriorly, 3/3 scales in lateral contact with postfrontals, one median azygous head scale, four postmentals.

Variation. Scale counts for the series of 51 *A. websteri* are shown in Table 1.

The dorsum of *A. websteri* is moderate to dark gray or brown. Head and body markings, if present, are generally dark and diffuse,

often disrupted. The nuchal patch is large and dark, with no white border. The scapular stripe is dark and short. The interocular bar is present in the lighter colored specimens, as is sometimes the case with the interparietal U and interocular V. Dorsal chevrons are always absent. The dorsolateral stripes are disrupted and diffuse. The limbs and tail are vaguely barred. The interparietal is yellow, but appears as a copper flake in preserved specimens. The venters are bright yellow to yellow-orange. The dewlap is uniformly orange or orange with a narrow yellow margin; hues noted for the dewlap are: P1. 9L7, P1. 9L8, P1. 9L10, P1. 10L8, and P1. 11K10.

A series of eight *A. websteri* from Pont Soudé is notable in the variation in dewlap color and modal scale counts. The dewlaps vary from orange (P1. 10L8) to mustard (P1. 12L7) to pale yellow (P1. 11L4). The venters are not so bright as other *websteri*. Modal scale counts differences for the series are: six scales across the snout; five loreal rows; and 3/3 scales in contact laterally with postfrontals.

Well outside its normal distribution, *A. websteri* was found in abundance 3.5 km NW Bon Repos, Dépt. de l'Ouest, in young native mahogany (*Swietenia mahagoni* Jacq.). Electrophoretic evidence indicates that it is slightly more similar to northern *A. websteri* than to southern specimens of that species. Presumably, *A. websteri* in this location was a recent introduction by man to an artificial habitat. Recent road improvement has led to the total destruction of the localized habitat (Webster, 1978a). No specimens were preserved.

DISCUSSION

INTERACTION OF THE "*ANOLIS BREVIROSTRIS*"— *ANOLIS DISTICHUS* COMPLEXES

Species of the "*A. brevirostris*"—*A. distichus* group often present contrasting dewlap colors in areas of contact or proximity. Such differences suggest that dewlap color may be important for species identification and reproductive isolation (Webster and Burns, 1973). Both body size and color appear to be important in *Anolis* species identification, especially in simple (e.g., two species) faunas (Williams and Rand, 1977).

The *A. brevirostris* complex is closely associated with four subspecies of *A. distichus*: *dominicensis*, *ravitergum*, *favillarum*, and *suppar*. In areas of sympatry "*A. brevirostris*" and *distichus* gener-

ally vary in body size, body color, and dewlap color. In brief, the associated subspecies have the following characteristics: *dominicensis*, males to 58 mm, females to 48 mm snout-vent length, dorsum bright marbled green to rich chocolate brown, dewlap usually pale yellow; *ravitergum*, males to 56 mm, females to 45 mm snout-vent length, dorsum ashy gray to dark tan to pale greenish, dewlap pale yellow to bicolored with an orange basal spot; *favillarum*, males to 54 mm, females to 47 mm snout-vent length, dorsum dark green, dewlap vivid orange centrally with narrow pale yellow edge; *suppar*, males to 54 mm, females to 44 mm snout-vent length, dorsum pale green, dewlap pale yellow to yellow-green, at times with a dull yellow-orange basal smudge. For more detailed descriptions, see Schwartz (1968) and Webster (1978b). In general, *A. distichus* is larger than "*A. brevirostris*" and the green and brown unmarked dorsa of *distichus* contrast with the gray and marked dorsa of "*brevirostris*".

A. caudalis is the only species within the *brevirostris* complex which is not extensively sympatric with *A. d. dominicensis*. Quite to the contrary, both mainland and Gonave *caudalis* appear to exclude *dominicensis*, except for two specimens, one from Trou Forban and another from nearby Ste. Philomène. At the disjunct populations on the Tiburon Peninsula, Grand Boucan *caudalis* also appear to exclude *dominicensis* and the Jérémie population is sympatric with another subspecies, *A. d. suppar*. No color notes exist for the Jérémie *caudalis*, nor can any be assumed. *A. caudalis* here is the smaller lizard and has two prominent markings. The nuchal patch is large and faint with a white border and the interparietal U is broad and dark.

A. d. dominicensis is broadly sympatric with *A. websteri* and *A. marron* throughout the latter's respective ranges. Locally *dominicensis* is precisely syntopic with *websteri*. *A. websteri* has the largest snout-vent length for the *brevirostris* complex and at this region of syntopy is larger than *dominicensis*. The reduced, borderless nuchal patch and generally vague and diffuse markings of gray-brown *websteri* probably indicate an increased reliance on dewlap color for species recognition and reproductive isolation. The orange dewlap of *websteri* sharply contrast with the typical pale yellow of *dominicensis* and white to gray-yellow with greenish basally of *A. caudalis*. The isolation is incomplete, for Webster (1978b) reports a low inci-

dence of hybridization at Montrouis with *dominicensis*; and (in litt.) some hybridization and introgression (two of five proteins, only one way, only a short distance) with *caudalis* at Trou Forban.

Though populations of *A. marron* are never far from those of *A. d. dominicensis*, no areas of syntopy are known. The dark olive-gray or bicolored tan with reddish center dewlap contrast with the pale yellow of *dominicensis*. The dark scapular stripe and large, dark, white bordered nuchal patch of *marron* are more prominent dorsal markings than those of *A. websteri* and may provide additional cues for species recognition and reproductive isolation. *A. marron* and *A. b. wetmorei* come in contact near Marigot. The bicolored pale yellow with orange basal spot of *A. b. wetmorei* contrasts with the *marron* dewlap.

In the eastern Cul de Sac Plain (Thomazeau; Manneville), *A. b. brevirostris* is sympatric (but apparently not syntopic) with *A. d. dominicensis*. Of the two species in the area, *A. b. brevirostris* is distinctly the inhabitant of the xeric scrub and *A. d. dominicensis* the inhabitant of more mesic situations (oases and cultivated areas). *A. b. brevirostris* is the widespread lizard in open areas, whereas *A. d. dominicensis* is restricted to certain less rigorous habitats and is in effect surrounded by *A. b. brevirostris*. Here, the dewlap color of *A. d. dominicensis* is atypically a deep orange (Pl. 4C11, Pl. 4G10, and Pl. 4G11), at times with a faintly brown cast (Schwartz, 1968). This contrasts strongly with the dewlap of *A. b. brevirostris*, which locally is dully pigmented with no conspicuous pattern in white to pale shades of yellow, gray-yellow, and gray-brown.

There is a clinal decrease in the amount of orange in the dewlap of *A. d. dominicensis* away from *A. brevirostris*, until at the southern edge of the Cul de Sac and Valle de Neiba plain, pale yellow is again the typical color of *A. d. dominicensis* dewlaps. It is important to note that in this area (Fond Parisien to Duverg ) *A. b. brevirostris* dewlaps are predominantly pale orange, dull orange, to bright orange.

Another subspecies, *A. d. ravitergum*, is sympatric with *A. b. brevirostris* at the latter's eastern distribution. Webster (1978b) reports hybridization locally at Balneario la Zurza, 5 km WNW Duverg . Here the dewlaps of *A. d. ravitergum* range from uniformly light yellow-orange to strongly bicolored with an orange basal spot. Dewlaps of *A. b. brevirostris* are all monochromatic

orange in varying degrees of intensity. Dewlaps do not appear consistently to differentiate these populations despite the strong dewlap color contrast.

A. b. wetmorei, like *A. caudalis*, appears to exclude *A. distichus* but is locally sympatric with two subspecies of *A. distichus* at three localities. *A. d. dominicensis* and *A. b. wetmorei* are sympatric at Belle Anse (=Saltrou), D  pt. de l'Ouest, and Las Mercedes, Pedernales Province. Here, *wetmorei* is bicolored with an orange basal spot and a yellow or cream outer margin. *A. d. dominicensis* dewlap is typically pale yellow but occasional specimens in the Sierra de Baoruco in Pedernales Province have the dewlap very pale yellow to practically white.

A. d. favillarum and *A. b. wetmorei* are sympatric at Hermann's finca, near Para  iso, Barahona Province. No color notes exist for the single specimen of *wetmorei* taken from this locality. (These are, however, old records and may not imply real sympatry.)

At all three of these widely separated localities, *wetmorei* is generally the lizard of the lower elevations with *distichus* occupying the moderate to higher elevations (300–1250 m) of the Massif de la Selle and Sierra de Baoruco.

A. b. deserticola is sympatric with one of three subspecies of *A. distichus* throughout most of its range. *A. d. dominicensis* and *A. b. deserticola* are widely sympatric in the Valle de San Juan from 7 km NW Vallejuelo and 15 km SE San Juan westward to the Dominico-Haitian border. The dewlaps of both are pale yellow except at Vallejuelo where *deserticola* is bicolored with a pale orange blush. *A. d. ravitergum* is sympatric throughout most of the remaining range of *deserticola* and in local situations is even syntopic (0.5 and 2.5 km E Cach  n). Webster (1978b) notes the similarity in dewlaps. Both are bicolored, with a pale margin surrounding a darker or brighter spot of variable size. Corresponding to this high degree of similarity is a higher incidence of hybridization at these localities.

A. b. deserticola extends onto the northern slopes of the Sierra de Baoruco, where in the intermediate altitudes and transitional vegetation it is sympatric and locally syntopic with *A. d. favillarum*. The dewlaps are here identical; both are dark orange, but the nuchal patch and gray dorsum of *deserticola* contrast strongly with the green dorsum of *favillarum*. The incidence of hybridization here has not been investigated.

The sample examined in this study represents the known distribution of the "*A. brevirostris*" complex. Three of the six populations recognized by scale counts correspond to the informal siblings A, B, and C of Webster and Burns (1973). *A. brevirostris* is restricted to Species C and the name *A. caudalis* is assigned to Species B as suggested by Williams (1976). The distribution of *A. b. wetmorei* of Isla Beata is expanded to include the Peninsula de Barahona and part of the southern coast of the Tiburon Peninsula. Species A (*A. websteri*), a new sibling species (*A. marron*), and a new subspecies (*A. b. deserticola*) are described. Scale counts were taken as supplementary evidence of geographic variation along with that in dewlap color within the *brevirostris* complex, and to provide a basis for the formal description of parapatric siblings.

A. caudalis and each of the three subspecies of *A. brevirostris* overlap in dewlap color variation. Dewlaps bicolored yellow with orange centers and/or uniformly pale yellow are found to varying degrees in the distribution of each species. *A. caudalis* is, by modalities of scale counts, the most readily distinguishable of these species and of the entire *brevirostris* complex. Modally, has six scales across the snout (all others four), preoccipital present (all others a single row of small scales bordering the interparietal anteriorly), and two median scales (all others modally one or bimodally one and two).

Webster (1978a) noted the presence of shared alleles of *A. caudalis* with *A. marron* and *A. b. deserticola*. The scale counts of the latter two populations differ from the former not only by the unique modalities of *caudalis* noted above, but further by the modes shared by *marron* and *deserticola*: scales between interparietal and supra-orbital semicircles 0/0 (all others 1/1); postmentals, bimodes five and six, with the highest mean values *deserticola* 5.8 and *marron* 5.6 (others, mode four or five, or trimode four, five, and six; means 4.7 to 5.3). Despite the wide geographic separation (ca. 120 km airline across the Sierra de Baoruco and Massif de la Selle at the closest points), these two populations have essentially the same scale counts. The modalities for the scale counts taken are the same, the percentages of the modalities are within three to 17% of each other, and the distribution of the non-modal counts is similar. Further, these are two of the three populations that are extensively sympatric with *A. distichus*. *A. marron* differs from *A. b. wetmorei* and the

entire *brevirostris* complex by its unique dewlap color (dark olive-gray to tan with reddish center).

A. b. brevirostris differs from other populations in the "*A. brevirostris*" complex by the unique modes of 3/3 scales in contact with postfrontals laterally (all others modally 2/2 or bimodally 2/2 and 3/3) and four postmentals, with 4.7 the lowest mean value (others modally five, bimodally five and six or trimodally four, five, and six; means 4.7 to 5.8).

A. b. wetmorei differs from other populations in the *brevirostris* complex by the unique bimode of 2/2 and 3/3 scales in contact with postfrontals laterally. *A. b. wetmorei* differs from the other subspecies of *A. brevirostris* in having modally five postmentals (*brevirostris* modally four and *deserticola* bimodally five and six), but share this characteristic with *A. caudalis*. Variation in scale counts and dorsum occur within *A. b. wetmorei*. At Enriquillo there is a dramatic change in vegetation and geography from the mesic slopes of the Sierra do Baoruco in the north to the arid plain that forms the southern tip of the Península de Barahona. This change appears to effectively inhibit genetic exchange between *A. b. wetmorei* populations demonstrated by Webster's observation of different frequencies for variants of three proteins and the modal shift in loreal rows and the dorsum coloration differences for the two regions documented by the present study. On the eastern coast of the Península de Barahona (Barahona to Enriquillo) *wetmorei* modally has five loreal rows and a greenish tan dorsum in association with the orange, red-orange, and bicolored orange with a thin yellow margin dewlap color. To the south and west (Oviedo to Marigot) *wetmorei* modally has four loreal rows and no greenish dorsa have been recorded.

A. websteri differs from other populations in the *brevirostris* complex by the unique trimode of four, five, and six postmentals (others modally four or five, or bimodally five and six). *A. websteri* and each of the three subspecies of *A. brevirostris* overlap in dewlap color variation. Dewlaps uniformly orange and bicolored orange with a thin yellow margin are found to varying degrees in the distribution of each species. The subspecies of *A. brevirostris* are further distinguishable from *A. websteri* by their unique modal scale counts noted above.

The distribution presented in this paper follows closely that of Webster and Burns (1973), but varies from that of Webster (1978a). Webster noted electrophoretic similarities between *A. caudalis* and the Jacmel-Marigot populations and between *A. caudalis* and the San Juan-San José de Ocoa populations. He implied that the Jacmel-Marigot populations be referred to *caudalis*. Here the southwestern Tiburon populations are designated as a new species, *A. marron*. For the *brevirostris* complex, *marron* varies greatly from *caudalis* in modal scale counts, dewlap color, and in relationships to *A. distichus*. Modal scale count variations are: scales across snout (four versus five), loreal rows (five versus four), scales between supraorbital semicircles and interparietal (0/0 versus 1/1), median head scales (bimodes one and two versus mode two), postmentals (bimodes five and six versus mode five), and preoccipital condition (modally a series of small scales bordering interparietal anteriorly versus preoccipital modally present). The dark olive-gray to tan with reddish centered dewlap of *marron* distinguishes it not only from *caudalis* but is unique in the whole *brevirostris* complex. *A. caudalis* excludes *A. distichus dominicensis* where *A. marron* and *A. distichus* are sympatric. Webster also noted shared alleles of *marron* with *A. b. wetmorei* at Bell Anse.

The northern Dominican populations having electrophoretic similarities to *A. caudalis* are designated as a new subspecies, *A. b. deserticola*. *A. b. deserticola* and *A. marron* have the same scale count modes, and thus the same substantial difference from *caudalis*. Webster (1978b) noted variation in hybridization of *A. distichus* with *A. b. brevirostris* from that with *A. b. deserticola*. However, neither this variation nor the electrophoretic similarities discouraged Webster from associating *deserticola* with *brevirostris*.

A. marron would then appear to be an extension of "*A. brevirostris*" from the Península de Barahona, a pattern found in other reptilian species (*Ameiva leberi*, *Ameiva lineolata privigna*, *Ameiva taeniura vulcanalis*).

APPENDIX 1

1) *Anolis brevirostris brevirostris*: Haiti, Dépt. de l'Ouest, Source Trou Caiman (MCZ 124737-49); Thomazeau (MCZ 13769-70, MCZ 59388-89, MCZ 124705); between Thomazeau and Manneville (MCZ 59381); Manneville (MCZ 59382-87, MCZ 63154-58,

MCZ 121777-78, MCZ 123125-55) Eaux Gaillées (MCZ 59943-48, MCZ 63159-71, MCZ 118790-92, MCZ 121096-101); Ganthier (MCZ 124706-22); *Dominican Republic, Independencia Prov.*, Las Lajas (AMNH 41456, AMNH 41458-59, AMNH 41461); La Descubierta (AMNH 41433, AMNH 41437-38); Las Baitoas (AMNH 50149-50, AMNH 50199, AMNH 50210-16); 8.8 km W Duvergé (MCZ 125541); 2 km SW Duvergé (UF/FSM 42738).

2) *Anolis brevirostris deserticola*: *Dominican Republic, Azua Prov.*, 4 km SW Sabana Yegua, 420 m (UF/FSM 42739); *Barahona Prov.*, Cabral (MCZ 58511-25, MCZ 58526-36); 5 km S Cabral (MCZ 58509-10); La Cueva (MCZ 58425, MCZ 58429, MCZ 58432, MCZ 58436); lower part of road to Polo (MCZ 125551-53, MCZ 128219-25); 7.5 km N Canoa (MCZ 125549-50); Sierra Martín García, 1540 m (UF/FSM 36971); *Peravia Prov.*, 2 km N San José de Ocoa (MCZ 107079-80); 1 km N San José de Ocoa (MCZ 128255-56); 1 km S San José de Ocoa (MCZ 126012-44); 2 km S San José de Ocoa (MCZ 128248-54); Río Limón, 8 km S San José de Ocoa (MCZ 107081-82); 5 km N Baní, 110 m (UF/FSM 36972).

3) *Anolis brevirostris wetmorei*: *Dominican Republic, Barahona Prov.*, Barahona (AMNH 41307-15, AMNH 41317, AMNH 41322, AMNH 51430, AMNH 51446, AMNH 51533, MCZ 58694, MCZ 93106, UF/FSM 42733-35, USNM Field No RIC 040037-43); aviation field, Barahona (AMNH 51508-22, AMNH 51525, AMNH 51527); Hotel Guarocuya, Barahona (MCZ 107083-86); 1.7 km S Barahona (MCZ 9311); SW Barahona (AMNH 51535-40); Paraíso (AMNH 51630-31); Hermann's finca, near Paraíso (AMNH 516145); Los Patos (MCZ 58559-60); *Pedernales Prov.*, Oviedo (viejo) (MCZ 58537-38); 2 km E turn to Cabo Rojo (MCZ 128215-18, MCZ 128258-59); 1 km SW Las Mercedes, 380 m (UF/FSM 42736); 2 km E Las Mercedes, 250 m (UF/FSM 42737); *Haiti, Dépt. de l'Ouest* Lan Banane, near Saltrou (MCZ 68685-90).

4) *Anolis caudalis*: *Haiti, Dépt. de l'Ouest*, 6.3 km N Duvalierville (MCZ 123072-99); Ste. Philomène (USNM 123351-56); *Ile de la Gonâve*, no other locality (MCZ 13783-89); Anse-à-Galets (MCZ 29046-50, MCZ 37507-16, MCZ 85299-309); Nan Café (MCZ 85225-45, UF/FSM 12286-1-9, UF/FSM 12287-1-9, UF/FSM 12288, UF/FSM 12290); Pointe à Raquettes (MCZ 25509-18, MCZ 80613-38, UF/FSM 12291-1-2); vicinity of Pointe à Raquettes (MCZ 80581-86); Ti Roche, 9.5 km Pointe à Raquettes (MCZ 80587-612); Nan Palmiste, 4 km from Pointe à Raquettes (MCZ

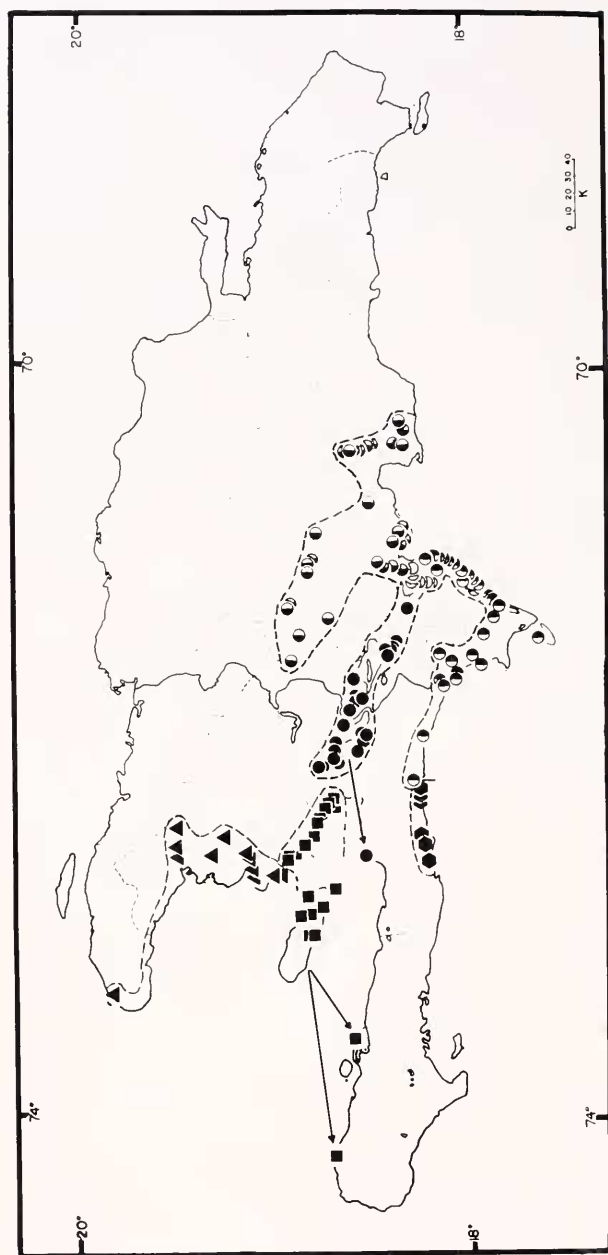


Figure 1. Map of Hispaniola, showing the distribution of the four members of the *Anolis brevirostris* group. Symbols for species are: *brevirostris*, circles; *caudalis*, squares; *marron*, hexagons; *websteri*, triangles. The three subspecies of *A. brevirostris* are indicated as: *A. h. brevirostris*—solid circles; *A. h. deserticola*—circles with left half blackened; *A. h. wetmorei*—circles with right half blackened. Note also the two arrows to the distal portion of the Tiburon Peninsula showing localities for *A. caudalis* at Jérémie and Grand Boucan, and the arrows showing the occurrence of *A. h. brevirostris* at Léogâne. The open circles between Barahona and Lago de Rincón, and including the northern slopes of the Sierra de Baoruco south of Cabral represent specimens that are intermediate between *A. h. wetmorei* and *A. h. deserticola*, but are closer to the latter.

80639-58); Nan Saline (MCZ 85169-74, MCZ 85175-81); Tête Source (MCZ 85182-205); Platon Yéyé (MCZ 85206-24); Lan Coupe (MCZ 85281-98); *Ile de la Petite Gonâve* (AMNH 49745, AMNH 49747-48).

5) *Anolis websteri*: Haiti, Dépt. de l'Artibonite, Marché aux Poteaux (MCZ 125117-25); Passe Reine, between Gonaïves and Ennery (MCZ 63141-42); Pont de l-Estère (MCZ 63135-40); bridge over Rivière de l'Artibonite, St. Marc road (MCZ 59355-80); Lafond (MCZ 118783-89, MCZ 123101-24, MCZ 125110-16); St. Marc (AMNH 42593, AMNH 49696, AMNH 49699-700, AMNH 49702-04, AMNH 49708-09, AMNH 49711-12, AMNH 77566, USNM 59219); Montrouis (MCZ 125126-69).

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